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Plant intelligence

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Abstract Intelligent behavior is a complex adaptive phenomenon that has evolved to enable organisms to deal with variable environmental circumstances. Maximizing fitness requires skill in foraging for necessary resources (food) in competitive circumstances and is probably the activity in which intelligent behavior is most easily seen. Biologists suggest that intelligence encompasses the characteristics of detailed sensory perception, information processing, learning, memory, choice, optimisation of resource sequestration with minimal outlay, self-recognition, and foresight by predictive modeling. All these properties are concerned with a capacity for problem solving in recurrent and novel situations. Here I review the evidence that individual plant species exhibit all of these intelligent behavioral capabilities but do so through phenotypic plasticity, not movement. Furthermore it is in the competitive foraging for resources that most of these intelligent attributes have been detected. Plants should therefore be regarded as prototypical intelligent organisms, a concept that has considerable consequences for investigations of whole plant communication, computation and signal transduction.

Introduction

“A goal for the future would be to determine the extent of knowledge the cell (organism) has of itself and how it utilizes this knowledge in a thoughtful manner when challenged” (McClintock 1984).

This statement was made by the plant biologist Barbara McClintock, in her Nobel Prize acceptance speech. It can be rephrased as follows. “A goal for the future would be to determine the structure of the current integrated

molecular network of the cell resulting from development and environmental experience (memory) and how that network acts to intelligently generate successful adaptive responses when challenged.” McClintock’s statement is a plea for better understanding of signal interpretation or signal transduction (challenge), how cells “know” both their stage of development and how it has been modified by environmental signals, and finally how thoughtful (intelligent) behavior is used to improve fitness through adaptive responses. The deliberate use of “thoughtful” indicates that McClintock like many plant biologists including Charles Darwin and Julius von Sachs observed plant behavior strikingly akin to intelligent behavior in animals. This article, about plant intelligence, challenges a common view that does not credit plants with intelligent capabilities. As advanced animals, our sensory systems operate on time scales of seconds and it is difficult to observe behavior that operates on hours or days that would be typical for many plants. Much plant activity is missed as a consequence and only with patient and continuous observation and time lapse photography (e.g. Attenborough 1995) is that perspective now changing. However, a lengthy time scale enables reversal of many developmental events as are found in the shedding of leaves, minor roots, branches and flowers. Furthermore permanent existence in two very different environments, the soil and the atmosphere constrains movement.

What biologists mean by intelligence is discussed later in this paper. But three important criteria must be introduced here. (1) Intelligence is complex adaptive behavior, even in humans, although not all behavior is intelligent (Stenhouse 1974). (2) Intelligent behavior involves the whole organism. (3) Intelligent behavior requires both an intelligent organism and crucially the environmental challenge for its expression. Plant biologists rarely impose situations on plants that would expose intelligent behavior (Trewavas 2003).

Adaptive behavior is designed to improve survival and reproduction and thus fitness. The whole life cycle may be the principal object of natural selection (McNamara and Houston 1996; Schlichting and Pigliucci 1998). There is a common relationship, well established in plants (but

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obvious in animals too), between acquired resources and reproductive success; in higher plants this equates to numbers of seeds and thus the potential numbers of siblings (e.g. Appleby et al. 1976). The contribution of intelligent behavior to ultimate fitness in plants may be best exerted in the competitive fight for resources (food).

This review indicates that visible plant behavior, that is phenotypic plasticity, (underpinned by physiological and molecular plasticity) is initiated in response to a complex of abiotic and biotic environmental signals. Much of this behavior results from the necessity for active foraging for resources of light, carbon dioxide, minerals and water in competitive circumstances but may have its basis in an ability to internally model the approach to potential rich sources of resources. There is no agreed definition of intelligence so instead the kinds of behavior that different biologists describe as intelligent in different systems and organisms are outlined. Using these descriptors of intelligence as a guide, the specific behavior of both roots and shoots in certain environmental circumstances is then discussed and it is concluded that many plants exhibit the necessary behavioral capabilities that others describe as intelligent.

Plant behavior and foraging: predictive modeling of future resource supply

Plant behavior is phenotypic plasticity—animal behavior is movement

Behavior can be defined as the response of organism to signals and is fundamentally different between most plants and animals (Silvertown and Gordon 1989). Several billion years back, the primordial plant cell solved the problem of energy acquisition by a symbiotic combination with a photosynthesizing, blue-green alga. Since light is ubiquitous over the surface of the globe the need for movement was no longer an evolutionary plant imperative. Instead the requirement to gather light, minerals and water drove the evolution of morphologies able to best occupy local space and thus food resources. A branching structure with tip growth and metameric repetitions of leaf plus bud and root meristems seems to be the biologically most efficient (Harper 1977; White 1984). Because plants are the basis of all food chains, a metameric structure advantageously enables ready recovery from herbivore or other damage; organ specialization was kept to a minimum for the same reason (Trewavas 1986).

But the qualitative and quantitative range of signals experienced by plants continuously changes as resources are exploited, growth continues and new territory is encountered. Consequently development continues throughout the life cycle and the phenotype of leaves, stems and roots is plastically adjusted to optimally exploit each new signal situation (Bradshaw 1965; Callaway et al. 2003; Jennings and Trewavas 1986; Schlichting and Pigliucci 1998; Sultan 2000). “Among plants (changes in) form may be held to include something corresponding to behavior in the zoological field” (Arber 1950).

The primordial animal cell satisfied energy requirements by eating plants but this required movement to find the food. With time and the development of the forcing evolutionary driver of predator–prey relations in animals, complex sensory organs, muscles to move and complex nervous systems to rapidly coordinate both activities, appeared. Improvements in the speed of catching engendered improvements in the speed of escape.

These qualitative developmental differences between plants and animals are crucial for understanding plant intelligence. Warwick (2001) has emphasized that it is essential to understand intelligence within the framework of the capability of the organism; the skill that any organism brings to solving the challenges in its environment and allows one species to dominate and exert power over other species. In plants much of that skill in problem solving involves adaptive changes in phenotype. Intelligence has evolved to improve survival and reproduction, and thus fitness.

Many signals modify the plant phenotype. Many abiotic signals are sensed by plants. For example, humidity, light, minerals, gravity, wind, snow melt, soil structure and composition, etc., and totaling about 20 in number, initiate phenotypic changes. Furthermore these signals are sensed and the intensity, the direction and the length of exposure are finely discriminated (Trewavas 2000; Turkington and Aarsen 1984). “If etiolated seedlings are placed between two sources of light differing so slightly that the differences cannot be detected by ordinary photometric methods, the seedling always bends promptly toward the source of the slightly more intense light” (Palladin 1918) is perhaps typical of the sensitivity plants bring to most abiotic signals. But higher plants integrate the signaling complex; they process the information and construct a composite response specific to the range and balance of perceived signals (Trewavas 2000). The complexity of the plant environment ensures that no response is autonomic (a behavioral term requiring complete replication under all circumstances).

Some plant scientists think that plant behavior is autonomic because on providing the same strength of signals and laboratory situation, the averaged response looks similar. But autonomic responses are fixed, they cannot vary according to circumstances. However it can be added that if a person was confined without water for 3 days, the intelligent response on placing water in the cage is entirely predictable but hardly what one would regard as autonomic. Plant scientists experimentally impose signals (such as water depletion) until they gain a reproducible response, a direct parallel to that of the thirsty human. In most signaling situations, no-one signal overrides all others.

One response that commonly figures in this argument is the text-book bending of seedling roots to the vertical vector of gravity when the seedling is initially placed horizontally. Because it is easy to demonstrate, it is always assumed to be entirely uniform and autonomic. But no such uniformity of response actually exists between individuals except as a statistical average (Trewavas 2003). More important is that the gravity signal can be easily over-ridden by touch and by gradients of moisture, light, temperature, oxygen and

other soil gases applied in different directions (Aphalo and Ballare 1995; Eapen et al. 2003; Massa and Gilroy 2003).

Equally important is the individuality with which each plant constructs its response (Trewavas 1998). Such behavior is normally disguised when statistics are inappropriately applied to responses and averaged over many plants (Trewavas 2003). Occasional photographs of large numbers of individuals exposed to the same signals indicate the enormous degree of variation in response (e.g. Bennett-Clerk and Ball 1951). But even cloned plants do not respond uniformly. Using different genotypes, derived from individual seeds, Bazzaz (e.g. p 168) reported the interactions between nutrient and light gradients on reproductive yield in the form of topological surfaces that clearly exemplify individual variation.

Biological signals and resource competition

Numerous biotic signals are sensed and modify the phenotype. These include the presence, absence and identity of neighbours, (Tremmel and Bazzaz 1993, 1995), cooperation, mutualism, disturbance, trampling, herbivory, parasitism and space (Callaway et al. 2003; references are listed in Turkington and Aarsen 1984). Since the phenotype differs with each new neighbour, the ecological niche is not a fixed quantity but like the phenotype itself, is plastic in character and changes as growth continues. Turkington (Evans and Turkington 1988; Turkington et al. 1991) indicates that even after moved to different soils, plants retain the memory of their original neighbours for several months up to a year.

But competition is more important than other biotic signals. It is easy to demonstrate the effects of competition by growing plants at increasing densities. Although, predictably, growth is reduced, the phenotypic changes are selective for only certain parts of the plant and vary according to the degree of competition (e.g. Darwinkel 1978). Despite the considerable contribution of Charles Darwin to botanical knowledge, the Darwinian struggle involving overproduction, selection and differential survival (Goldberg and Barton 1992; Gould 2002) attracts limited attention from ecologists (Aphalo and Ballare 1995) and almost no interest by physiologists. The Darwinian goal of any individual plant is to maximize fitness within the constraints of the local environment and genetic potential. From this framework there must be a resource fight with neighbours as well as counterbalances to environmental insults. Genes in this context should be seen as only constraining the range of possible future phenotypes, not as rigidly specified phenotypic information (Sultan 2000). Darwin (1859) was quite clear as to the relevant importance of biotic and abiotic factors. "There is a deep-seated error of considering the physical conditions of a country as the most important for its inhabitants, whereas it cannot be disputed that the nature of the other inhabitants is generally a far more important element of success."

Signal transduction in plant cells

How information is processed or transduced inside cells, is important to understanding plant intelligence. In plant cells the core of signal transduction events is platformed on an interactive network composed of over a thousand protein kinases and protein phosphatases and numerous second messengers (Gilroy and Trewavas 2001; Trewavas 2000; Trewavas and Malho 1997). Connections within the network generate emergent properties that currently are ill-understood but they provide for simple decisions that coherently interacting together with other cells generate emergent tissue and in turn whole plant behaviors. Information flow leads to modifications of gene expression and changes in ion flux modify turgor pressure. The critical feature in all such transduction networks is the ability to alter the strength of connections and thus control the direction of information flow (Vertosick 2002). Learning requires the enhancement of particular pathways of information flow through the network; memory is simply, in turn, the semipermanent modifications in the speed and direction of the flow of information thus induced by learning. Learning and memory are thus interrelated. In addition numerous other proteins from genes representing probably up to one quarter of the genome either modify substituents of the basic kinase network or form connected signaling complexes of their own. Protein-protein interacting networks have been constructed for yeast but currently these only show the network anatomy (Gavin et al. 2002; Maslov and Sneppen 2002; Perkel 2004; Ravasz et al. 2002). What is now required is the more difficult network physiology. The transduction complex constituents in plants are very similar to those used in animal cells and nerve cells (Gilroy and Trewavas 2001).

Plant actively forage for environmental resources by modeling their future availability and benefits over costs

The basic requirements for plant growth are light, carbon dioxide, some 10 or more minerals and water. However in wild situations the presentation of these resources can be extremely patchy, pulsatile and frequently appear as gradients varying in intensity (Bell and Lechowicz 1994; Farley and Fitter 1999; Grime 1994; Kupperts 1994; Pearcy et al. 1994; Robertson and Gross 1994). Soil mineral distributions depend on previous plant exploitation. Clonal plants using stolons or rhizomes sample the mineral distribution as they explore the soil and assume different morphologies, long and thin when resources are scarce, short and fat when abundant (Aphalo and Ballare 1995; Hutchings 1997; MacDonald and Leiffers 1993). Many trees are constructed from long and short shoots, the long being exploratory for new light sources in a canopy of light patches, whilst short shoots carry most of the leaves and exploit light already available (White 1984). Light intensity is dependent on cloud variability and canopy gaps as well as self shading and shading from other plants. Growing roots rapidly

develop mineral exploitation shells around themselves requiring further root growth to properly exploit soil resources (Grime 1996). Water is also frequently presented to roots as gradients because of the variable distribution of organic water-retaining material, sand, clay and stones.

Plants actively forage for food resources in the resource mosaic by changing their architecture, physiology and phenotype (De Kroon and Hutchings 1995; Evans and Cain 1995; Grime et al. 1986; Grime 1994; Hutchings and De Kroon 1994; Slade and Hutchings 1987). The goal is not just acquisition but in many cases denial of these resources to surrounding competitors. This realisation has been a major advance in understanding plant behavior. When exploration finally encounters rich nutrient patches, both roots and shoots proliferate enormously, greatly increasing both the surface area of absorption and the relative residence time in this region (Drew and Saker 1975; Granato and Raper 1989; Harper 1977; Henriksson 2001; Jackson and Caldwell 1989; Wijesinghe and Hutchings 1999). However, exploitation shells rapidly develop around roots and thus continued root growth and proliferation is essential if the resource is to be efficiently gained (Grime 1994). Increased proliferation is usually confined to the region experiencing the resource abundance. Although some beneficial effects on overall growth might result, more important is the acquisition and storage of resources that can be used later to provision seeds and increase fitness. When rich resources are encountered one result is increased exploratory activity based presumably on the prediction that other rich sources may be nearby.

It is growth along gradients of resources that lead both root and shoot to eventually meet rich pockets (Fig. 1). Exploratory shoots will grow along light gradients to the more intense regions and roots will grow along humidity and mineral gradients. Information transduced by resource sensors thus directs behavioral responses that increase the probability of attainment of richer sources of food in the near future. If the gradient changes direction then the new situation must be modeled on the transduction network and the model retained whilst overseeing the changes in direction. In roots and shoots this may require model retention for more than several minutes.

Changes in the rate of receptor occupancy are calculated and modelled by the information processing circuitry.

When critical thresholds are passed, intense shoot and root branching commences (Aphalo and Ballare 1995; Callaway et al. 2003; Gersani and Sachs 1992; Harper 1977). But this is a speculative enterprise. Leaves do not transport fixed carbon until nearly mature; instead they act as a speculative drain on the limited supplies of root minerals and water (Taiz and Zeiger 1998). Likewise roots only sequester minerals in their mature regions. Inaccurate speculation, that is poor decision-making, can waste valuable resources and short shrift can be expected in the Darwinian struggle. The growing shoot and root must retain their model of the predicted future resources for several days to oversee these phenotypic changes and until the new leaves and roots start to transport resources to the rest of the plant.

“The *sine qua non* of behavioral intelligence systems is the capacity to predict the future: to model likely behavioral outcomes in the service of inclusive fitness” (La Cerra and Bingham 1998). This statement was made in respect of bacteria chemotactically swimming along a resource gradient and root and shoot growing along resource gradients are a direct parallel. The term “predictive modeling” is used in this article to describe this behavior. In recurrent and novel environmental situations, individual cells, tissues and whole plants model the cost/benefits of particular future behaviors, so that the energetic costs and risks do not exceed the benefits that adaptive behavior procures. Such modeling takes place on an adaptive representational network that is an emergent property arising from cellular signal transduction and whole plant interactive networks. Predictive modeling is found even in primitive forms in bacteria, is more complex in plants but is most accurately exemplified in complex brains (La Cerra and Bingham 1998). Many higher plants are thus typical of behavioral intelligence systems.

It is in foraging that animals express much intelligent behavior because, like plants, resource acquisition is also crucial to fitness. Analogously food is sought by exploratory activity and once found, longer time is spent in consumption. Given the different potentials of the two kinds of organism, the activity is identical. McClintock’s “thoughtful” response appears most strongly in the hunt for resources.

Fig. 1 (a) Proliferation of tissues when rich sources of resources are encountered. This figure shows a whole branch of holly that had grown about 2 m through a yew bush (b) This figure shows about a metre of this branch cut out. As the branch approached breakthrough point, the numbers of leaves at each node increased until breakthrough was achieved and massive proliferation of leaves resulted



Biological views of intelligence

“Part of the trouble is that nobody knows what artificial intelligence is. In fact nobody even knows what intelligence is” (Goodwins 2001). There are many views about the nature of intelligence but no agreement as to its meaning (Warwick 2001). The term almost certainly encompasses a variety of different behavioral traits which when integrated together produce intelligent behavior concerned with problem solving (Warwick 2001). Dictionary definitions taken from psychological models are limited to human intelligence and include properties such as reasoning or sentience. In their unelaborated and simplest form, these can be recognised as assessment involving memory and self-recognition. But most biologists are not psychologists and in their search for the origins of intelligent behavior, much wider perspectives are necessary. The English word, intelligence, derives from the Latin, *inter legere* meaning simply, choice.

A common assumption is that only animals with brains can be intelligent. This as pointed out by Vertosick (2002) is simple brain chauvinism, whilst the psychologist Schull (1990) asserts this view to be both anthropocentric and asserting nerve cells as possessing some sort of vitalist quality. Warwick (2001), an artificial intelligence expert also considers this to be “subjective intelligence.” He states that “Comparisons are usually made between characteristics that humans regard as important. Such a stance is biased and subjective. The success (fitness) of a species depends on it performing well in its own particular environment and intelligence plays a critical part in its success.”

Some biological views of intelligence are indicated below.

1. *Species intelligence* (Schull 1990). “Plant and animal species are information processing entities of such complexity and adaptive competence that it may be fruitful to consider them intelligent.” In a detailed argument, critically assessed by his psychological peers, Schull draws parallels between learning and natural selection, foresight with genetic assimilation, memory with knowledge of ecological niche.
2. *Immune intelligence*. “The immune system learns patterns, then uses pattern recognition to craft intelligent responses to novel threats.” “The ability to store and retrieve large sets of three-dimensional data requires some form of sophisticated long term memory—a type of memory typically associated with brains.” “The immune system must extrapolate from past experiences and react to novel situations using past experience as its guide” (Vertosick 2002). Antibodies to new antigens are constructed by gene shuffling and those with highest affinity for the antigen (the most fit) are specifically selected and replicated. The immune system “foresees” future bacterial evolution (DeCastro and Timmis 2002; Vertosick 2002; Vertosick and Kelly 1991).
3. *Bacterial intelligence*. “This simplest of animals exhibits a prototypical centralized intelligence system that has the same essential design characteristics and

problem-solving logic as is evident in all animal intelligence systems including humans” (La Cerra 2003). This statement was made in reference to bacterial chemotaxis. “Some of the most fundamental features of brains such as sensory integration, memory, decision making and the control of behavior can all be found in these simple organisms” (Allman 1999). Quorum sensing with communication is now known to generate emergent properties (Miller and Bassler 2001; Park et al. 2003a, b). Chemotaxis toward sugars or amino acids exemplifies choice.

4. *Protozoan intelligence*. Presented with a maze involving routes of different lengths with food at the end, *Physarum* always chose the shortest route indicating an ability to optimise energy gain whilst minimising economy of effort and thus predictive modeling. This “implies that cellular materials can show a primitive intelligence” (Nakagaki et al. 2000). Paramecia prefer small ciliates to bacteria but will eat bacteria if no choice is available (Corning 2003).
5. *Intelligent genome*. Thaler (1994) discusses the critical experiments of Cairns et al. (1988) that implied a neo-Lamarckian induction of mutation by antibiotics in the genes conferring resistance using the term intelligent genome for such behavior. Durrant (1962, 1981) reported some years back that treatment of flax plants with particular combinations of minerals would induce bushiness (as might be expected) but that this bushy character survived some 12–14 inbred generations before reverting to the original morphotype. The phenomenon of plant maternal effects on sibling behavior has been described several times (e.g. Agrawal et al. 1999). Plants contain intelligent genomes too.
6. *Metabolic intelligence*. A number of researchers have indicated how steps in metabolism have characteristics analogous to simple Boolean computer logic gates. Coupled with a network constructed from metabolic processes and protein protein interactions, intelligent capacities by single cells becomes explicable (Arkin and Ross 1994; Bray 1995; Okamoto et al. 1987).
7. *Swarm intelligence*. Colonies of social insects are constructed from large numbers of workers in communication with each other. Although no individual contains all the information necessary, a remarkable range of building, aggressive, harvesting or space assessment activities can be induced by simple changes in communication amongst all the individuals (Bonabeau and Meyer 2001; Bonabeau and Theraulaz 2000; Bonabeau et al. 2000; Franks et al. 2003; Seeley 1995). “It is not too much to say that a bee colony is capable of cognition, in much the same sense that a human being is. The colony gathers and continually updates diverse information about its surroundings, combines this with information about its internal state and makes decisions that reconcile its well being with its environment” (Seeley and Leven 1987). Plants gather and continually update information about their surroundings, integrate this with information about their internal state and make decisions that reconcile their well-being with their environment and are thus capable of cognition.

8. *Animal intelligence.* Animal intelligence controlled by a brain is known to be an emergent property resulting from complex communication between a network of nerve cells. In the snail, *Aplysia*, learning results from the construction of new connections (dendrites) and memory of that learning process disappears as the new dendrites decay (Kandel 2001). Communication between nerve cells is largely chemical (Greengard 2001) and about 100 different chemicals are used.

Summary on biological views of intelligence

In Sects. 1–7 intelligence is a property of the whole system and is thus decentralized. Only in section 8 is intelligence more discretely localised to a particular tissue, the brain, that then acts as a repository of control and information flow even over immune systems. All these forms of intelligence are underpinned by a network of interacting communicating elements (molecules, cells, individuals) in which the strength of connections can be altered redirecting the flow of information. That seems at present to be the critical requirement for intelligent behavior (Vertosick 2002).

The properties biologists recognise as exemplifying intelligent behavior are: information sensing, processing and integration; decision making and control of behavior; learning; memory; choice; self recognition; foresight by predictive modeling and computation to optimise resource acquisition with economy of effort. Some (or even many) plants possess all of these capabilities. A generic term that probably covers all these properties is a capacity for problem solving, dealing with problems that arise from the requirements of efficient foraging in recurrent and novel environmental situations.

Intelligent behavior of plants

“I have repeatedly had cause to refer to certain resemblances between the phenomena of irritability in the vegetable kingdom and those of the animal” (Sachs 1879).

“The tip of the root acts like the brain of one of the lower animals.”

“In several respects light seems to act on plants in nearly the same manner as it does on animals by means of the nervous system” (Darwin 1882). Darwin and von Sachs were leading experimental botanists of the nineteenth century and these quotations summarise their own experience.

Individual plants (genet) are a social organisation of numerous foraging organs that interact (competition, cooperation) with each other to form a network (Aarsen 1995; Gersani and Sachs 1992; Harper 1977; Sachs et al. 1993) and share many organisational properties in common with social insects (Trewavas 2005). In turn tissue properties emerge from the interactions between millions of cells each capable of simple information processing and behavior. The intelligence of ant and bee colonies emerges from the interactions between millions of workers whose individual behavior obeys certain simple rules. Much of

the control and assessment of these cellular interactions in plants may reside in the cambium and pericycle, meristems that are a kind of inner skin or sheaths investing the whole plant and in which communication is known to occur over long distances (Trewavas 2005). Furthermore by controlling vascular activity the cambium and pericycle can in turn control the activities of branches from the main shoot and root.

Although the metameric organisation of a plant is of a looser kind than the unitary animal (Harper 1977; White 1984), many cases of whole-plant adaptive decisions in response to signals, are present in the literature (Evans and Turkington 1988; Turkington et al. 1991; Kupperts 1994; Hartnett and Bazzaz 1983, 1985; Novoplansky et al. 1989; Trewavas 2003, 2004; Turkington and Klein 1991). Grafting is a typical illustration of whole plant communication. The root stock can specifically modify many shoot characteristics, such as branching, height, yield, bud formation, winter hardiness, disease resistance and leaf color. Homeo-box proteins amongst other root-produced signals (Kim et al. 2001) are now known to exert the necessary morphological and physiological controls on the shoot.

The construction of intelligent root networks and the recognition of self

By providing two individual plants of the same species with the same amount of mineral and water resources but different soil volumes, it has been found that the individual growing in the larger soil volume is substantially bigger (McConnaughay and Bazzaz 1991, 1992; Schenk et al. 1999). Individual plants sense soil space (and thus soil volume) probably resulting from an ability to sense how their individual roots are placed with respect to each other to minimize self-competition; once that condition is sensed, increased growth is the consequence. Some overall coordinating mechanism of root distribution seems likely to be involved, including self-recognition. Examination of excavated root systems confirms these observations (Callaway et al. 2003; Huber-Sannwald et al. 1997; Mahall and Callaway 1992). Growing plant roots preferentially occupy vacant soil and deliberately avoid the root systems of competing, alien individuals. If roots of different individuals of the same species are forced to contact each other, decisions are then made to rapidly cease growth of the touching roots (Callaway et al. 2003).

Gersani et al. (1998, 2001) set up a simple two-box experiment in which one individual plant was grown with roots split between the two boxes. One box of these “fence-sitter” plants were then exposed either to no competition, or to increasing numbers of alien competitors. In an entirely intelligent fashion, the fence-sitter moved its growing root systems from the pot with competition, to that free of competition and in proportion to the number of competitors. In further simple experiments individual plants were forced to competitively “share” the same soil with another individual (Gersani et al. 2001; Maina

et al. 2002). In this case recognition of competition led to enhanced proliferation by both individuals in their own soil in order to “steal” nutrients from their neighbour. But enhanced root proliferation led to a trade-off with reduced seed number thus decreasing fitness for both individuals. “Sharing” plants developed more and longer lateral roots, vectorially directed toward neighbouring roots than toward roots of the same plant, thus guarding their own territory (Falik et al. 2003; Gruntman and Novoplansky 2004; Holzapfel and Alpert 2003). In this competitive situation the plant better able to guard its own territory and to sequester more efficiently root resources will succeed better in the Darwinian battle. Such plants are clearly territorial, a word normally applied only to animals (Schenk et al. 1999).

For situations in which the individuals are from different species, an ability to vigorously compete (and out-compete) others in the hunt for root resources and increase seed number indicates that plants assess and respond to local opportunities that will, in the future, maximise benefit for the whole plant (Falik et al. 2003). This is another example of intelligent predictive modeling. The transduction mechanisms that respond quickly to aliens, increases the probability of future individual success and fitness. What information is passed between different individual plants to enable recognition is currently unknown.

The notion of self-recognition has been strikingly confirmed by growing individual seedlings containing two identical shoots and two identical roots. By surgical separation into one shoot/one root individuals, twins are produced that are clones of the original parent seedling (Gruntman and Novoplansky 2004). Do these separated twins still recognize each other, or do they now react as though the other is alien inducing enhanced proliferation of root tissue when grown together? After several weeks of separation, such “twins” were made to share soil. Both twins proliferated more and longer root systems than control seedlings indicating their twin is now recognized as an alien. This mechanism of self-recognition is not understood but since species contain millions of individuals it suggests that self-

recognition must be complex and is an important aspect of prototypical intelligent behavior in plants.

Future shoot formation and light foraging indicate intelligent behavior

The morphology of many plants is constructed so as to minimize self shading, perhaps in the same way that branch and lateral roots are optimally separated (Ackerley and Bazzaz 1995; Honda and Fisher 1978; Yamada et al. 2000). Leaves possess two light sensitive organs (the petiole and the pulvinus) that control the direction of the leaf lamina, ensuring it is intelligently placed at 90° to the prevailing polarity of incident sunlight, thus capturing maximum energy (Fig. 2) (De Kroon and Hutchings 1995; Muth and Bazzaz 2002a; Palladin 1918). These same two organs are also able to move the lamina out of the direct plane of sunlight if the light becomes too intense and becomes damaging. Within canopy openings, not only leaf position but branch polarity is constructed to align with the primary orientation of diffuse light (Ackerley and Bazzaz 1995). The direction in which new branches are formed in these circumstances is another example of predictive modeling increasing the probability of acquisition of light energy in the near future.

When plants are grown in competition however, simple patterns of leaf placement and minimal shading are often destroyed implying, perhaps, unknown mechanisms of leaf and branch self-recognition (Fig. 2) (Trewavas 2005). It is common for branches to become overgrown by other more competitive species. In these cases either minimal root resources are provided or more commonly the branch dies and the vascular system is sealed (Franco 1986; Honkanen and Hanioja 1994; Henriksson 2001; Jones and Harper 1987; Muth and Bazzaz 2002b, 2003). Carbohydrate (captured energy from more productive branches) and root resources are directed away from unproductive tissues and donated instead to productive organs to optimise energy acquisition and minimize energy outlay under competitive circumstances. The cambium is probably the decision

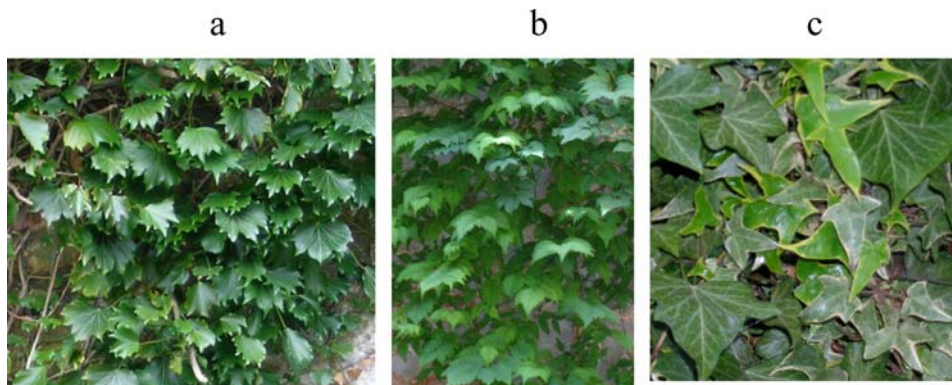


Fig. 2 Distribution of leaves on ivy. **a** This figure shows a familiar ivy mosaic. Examination of the leaf stalk (petiole) under the leaves indicates that the stalk can choose a direction within a 180° circle. The pulvinus (the attachment of the stalk to the leaf blade) then rotates the lamina to lie at right angles to the average directional polarity of

sunlight. **b** This figure indicates what happens when the polarity of sunlight is mainly vertical (*directly from above*). **c** This figure indicates that where two different ivy plants overlap, the mosaic pattern breaks down and leaves are placed competitively on top of the other competitor alternating in turn

arbiter over shoot branching and maintenance patterns (Sachs et al. 1993).

By analyzing experimentally the decisions that determine the distribution of root resources to different branches, it is clear that what is perceived is future branch vigor; much as shares are speculatively invested in companies that are thought likely to grow more quickly. These important decisions involve contributions from the whole plant and are further examples of predictive modeling (Novoplansky 1996, 2003; Novoplansky et al. 1989). Adaptive decisions that will increase the collection of resources and thus ultimately fitness, depend on the speculatively expected rather than the prevailing conditions. A striking example of predictive behavior is exemplified by the Mayapple (and no doubt other forest floor plants) that makes decisions about branching or reproduction 1–2 years in the future. The assessment is made on a complex of present-day developmental and environmental assessment with the prediction that present day conditions won't differ too much in the future (Geber et al. 1997). Many trees determine flower numbers a year in advance and if the spring is cold or water deficient, flower buds are simply abscised to adjust potential fruit production with predicted summer circumstances.

Plants intelligently optimise energy gain whilst minimising resource outlay

The clearest example of predictive modeling behavior can be found in a parasitical non-photosynthetic plant, Dodder. Upon touching suitable hosts, the stem coils around the host and subsequently haustoria develop which penetrate the host and remove carbohydrate, minerals and water (Kelly 1990, 1992). However numerous decisions are made on first contact. Many suitable hosts are rejected within a few hours of the first touch contact, indicating choice. But the reasons for rejection are only partly understood. Rejection can be reduced but not eliminated by increasing the nitrogen content of the host. But if the decision is made to parasitize, a predictive assessment is then made of how much nutrient can be gained from a successful host. In turn, this assessment is revealed by the final total length of the coils. There is thus an optimisation of resources invested before any nutrient is subsequently removed indicating predictive modeling.

A model developed by Charnov (1976) described how animals minimized their investment of energy against the energy gained during foraging and many animals fit this simple optimization rule (economy of effort). Using different hosts, Kelly showed that Dodder fits the Charnov (1976) model of animal foraging; that is, least energy is expended (in coiling) for maximal energy gain in different foraging situations. Such assessments require the ability to model an adaptive representational network that determines the final coil length. Least energy expended for maximal energy gained was exemplified by the case of *Physarum* above and this behavior was described by Nakagaki et al.

(2000) as intelligent. Studies on other plants indicate that the Charnov rule may be more general (Wijesinghe and Hutchings 1999; Gleeson and Fry 1997). Dodder does not parasitize itself indicating self-recognition.

Future changes in resource availability are also predicted and acted upon

It has been known for some years that light reflected from green vegetation has an enhanced far red/red (FR/R) ratio and contains more blue light than normal sunshine. Many plants perceive these parts of the light spectrum and thus model the possibility of future, not current, shading from competitors and thus future reductions of available light energy (Aphalo and Ballare 1995; Ballare 1994, 1999). Currently three avoidance responses to this situation have been observed. (1) New branches grow away from the direction of higher FR/R, as in *Portulaca* (Novoplansky et al. 1990). (2) The whole plant moves away as in the Stilt Palm by differential growth of prop roots toward the light (Trewavas 2003). (3) Apical dominance is increased, the main stem elongates more quickly with longer spaces between leaves which are larger in surface area with longer petioles and fewer more vertically erect branches (Aphalo and Bellare 1995). These phenotypic changes help to increase fitness in the plants that respond, by ensuring that light foraging is optimized under these more difficult competitive circumstances.

When young trees were provided with water only once a year, over the next several years they learned to predict when the water would be supplied and synchronised their growth with its appearance (Hellmeier et al. 1997). Again this an obvious case of predictive modeling followed by fitness changes in growth and development. Although comparisons between the organizational rules governing social insect colonies and plants will be the basis of a future article, there is an interesting parallel with experiments by von Frisch who wanted to examine whether bees were capable of learning (described in Corning 2003). He trained bees to come to a saucer of sugared water and once trained, on successive days moved the saucer defined distances and direction away only to find after some 4 days that the bees had predicted the next move of the saucer and were already waiting for the new position. Von Frisch concluded that bees could learn in this new situation and a similar conclusion can be drawn about plant behavior.

The intelligent approach to deal with light competition is to outgrow competitors. But to increase stem height reduces essential carbohydrate resources, ensuring there are less food resources to provision seeds. Fitness is thus reduced. The well-known evolutionary solution has been the introduction of long juvenile periods (as in trees) until the competition was overgrown, sufficient access to light guaranteed and reproduction could then be initiated. There are plants that have their height genetically fixed and such species were described by Givnish (1982) as altruistic when growing together. But application of Game Theory

analysis suggests that these species are out-competed in the resource battle by plants whose individuals instead plastically invest resources in variable height (Scheiving and Poorter 1999). Circumstances in these cases determine intelligent responses.

An alternative solution to the problem of light competition is to use sensitive stems, tendrils, petioles or roots (Darwin 1882) to climb on other plants. This strategy obviates much of the fitness penalty of heavy carbon investment in the stem that woody perennials have to accept. Those with tendrils will often not climb on their own stems or coil around other tendrils from the same individual (Darwin 1882, 1891; von Sachs 1879) indicating both the phenomena of self-recognition and intelligent placement of new leaves. These two authors reported that tendrils could unwind thus enabling adverse coiling decisions to be reversed. But tendrils seem also able to perceive alien plant supports (probably through FR/R imaging) and can generate changes in circumnutation so that they move toward them.

Once they encounter a suitable live host support, competitive overgrowth is now possible denying much light energy to the host (Baillaud 1962).

How plants learn

The simplest way of detecting whether plants can actually learn, is to place them under novel circumstances they will not have experienced during evolution and observe whether they successfully accommodate and continue development. Fortunately many such situations have been described in the past. Calabrese and Baldwin (2001) applied phosphon D at different concentrations to peppermint plants so creating the required novel situation (Fig. 3a). Although growth initially diminished at higher doses during the first few weeks, growth not only recovered, but after several weeks overcompensation of growth resulted and the treated plants were observed to grow much faster than controls. The plants

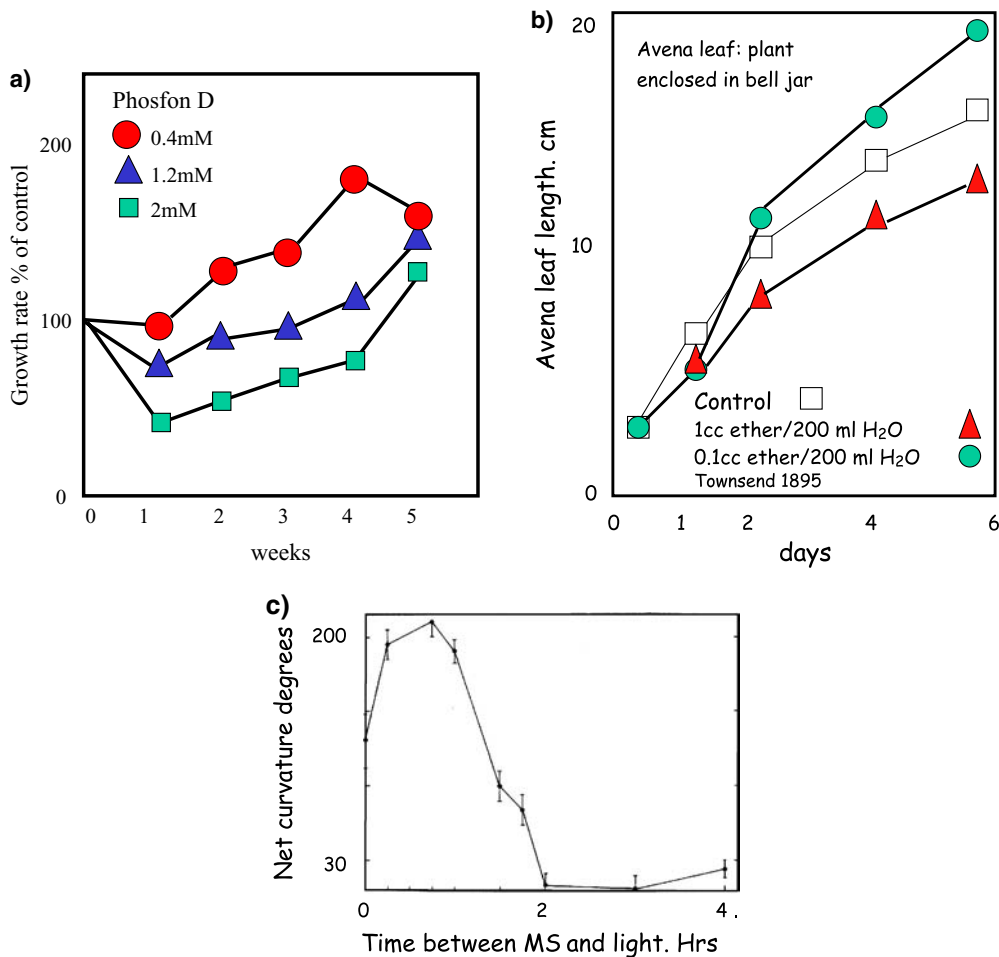


Fig. 3 Examples of learning and memory in plants. The simplest way to find if plants can learn is to provide circumstances they have not met before and see how they respond. **a** In this figure a peppermint plants were treated with various concentrations of a herbicide phosphon D and growth rates measured every week after treatment and expressed as a percentage of control plants. Note that at the lowest concentration the effect of the herbicide is actually to promote growth with the other doses following suit but later. **b** Oat plants

grown in an atmosphere provided by two different concentrations of ether in water. Note accelerated leaf growth at the lowest dose and inhibition at the higher. **c** An example of accessible memory. Tendrils require both mechanical stroking and blue light to curl. If the mechanical stimulation is given in the absence of light but blue light applied at various later times then the memory of the mechanical stimulation can last up to several hours, a time normally required for coiling

learnt to deal with the herbicide and overcompensated in order to place development and the life cycle back on track. Many other examples that have used other herbicides as novel environment generators illustrate the potential generality of this phenomenon (Appleby 1998). Many organic chemicals or solvents at low dose have been reported to accelerate growth (Fig. 3b; Moskwa and Ber 1951) or can break seed and bud dormancy and increase root formation (Trewavas 1992). In addition respiratory inhibitors and SH group reagents, can be used to create new learning situations for any plant and these too have effects, accelerating root formation or breaking dormancy.

There are many stressful treatments that will normally kill plants that experience them. These include high cadmium, salt, osmotic stress or high or low temperature, or mechanical stress. However, plants can be trained to survive such deadly treatments by previous exposure to milder stresses so that they learn how to accommodate the full blown treatment (Amzallag et al. 1990; Baker et al. 1985; Brown and Martin 1981; Henslow 1895 (The adaptation to mechanical stress is described on page 204 but is derived from a description by Pfeffer.); Laroche et al. 1992; Zhong and Dvorak 1995). Several stages can be recognized in this process. Mild treatments with the above signals will require changes in ion flux (phosphorylation is the most likely mechanism) to accommodate alterations to turgor and are easily reversible. Stronger treatments necessitate changes in gene expression to enable physiological and metabolic adaptation, whilst stronger-still involves phenotypic changes. These parallel the stages involved in animal learning with very short-term, quickly reversible learning resulting solely from ion flux changes; longer-term changes involve new dendrites, new protein synthesis and alterations in the morphology of the brain (Trewavas 2003).

Examples of plant memory

A number of plant developmental changes require two signals for completion. By giving one signal without the other, the length of time the memory of that one signal lasts, can be easily established (Desbiez et al. 1984, 1991; Jaffe and Shotwell 1980; Marx 2004; Trewavas 1999; Verdus et al. 1997). Thus, for example tendrils require both a mechanical stimulus and blue light to coil (Fig. 3c). By separating the time of application of the two signals the length of the memory of one signal can be determined. In this case the mechanical stimulation is remembered for several hours and is a meaningful memory in terms of the response of the tendril that also takes several hours to coil. Plant memory can last seconds, minutes, days, weeks and months according to the time frame of the signal and the developmental response examined.

Conclusion

This article has indicated that plants exhibit all of the properties listed earlier which are associated with the presence

of intelligent behavior. The examples provided in this article indicate that plants are capable of detailed sensory perception, information-processing and integration, decision-making and the control of behavior, learning, memory, choice, self-recognition, foresight by predictive modeling and computation to efficiently sequester resources. The question then arises as to why these have not been recognized earlier. The difficulties in different time scales between plants and animals have already been mentioned but such differences do make it difficult to see intelligent behavior without fairly precise long-term observation and measurement. It is only recently that ecologists have come to use the term foraging, because so much previous study simply used pot-grown and greenhouse-grown plants in which resources were freely applied. Many of the examples I have included in this chapter are concerned with the competitive foraging by both roots and shoots and the need to recognize the goal of fitness that is related to the capacity to acquire them. In animals it is easy to observe purposeful movement and this enables a simple start to make deductions about intelligent behavior in foraging. Whereas the presence of fundamental drives to obtain energy and water pass almost without comment in animals (i.e. hunger and thirst), because we experience them ourselves, such drives are equally present in plants but these can only be detected when the supply is very limited and strong competition is exerted to acquire them. These fundamental drives are part of the general property of homeostasis in animals (Cannon 1932); in plants they are part of the general and fundamental drive to complete the developmental life cycle and should be considered instead part of homeorhesis (Waddington 1957).

Accepting that aspects of intelligent behavior exist in plants, the question then arises as to how this is accomplished. "Plants have evolved an integrated complex of hormonal systems—a coordinated but non-centralized intelligence system that manages resources" (La Cerra and Bingham 2002) and we know that such communication is complex involving a plethora of communicating macro- and micro-molecules and electrical signals (Trewavas 1999, 2003). The integration of groups of patchy stomatal responses enables leaves to compute emergent but optimised leaf water relations (Peak et al. 2004). Patchy responses by groups of plant cells have been reported several times (Trewavas 2003). The model provided by Peak et al. (2004) suggests directions in which an understanding of plant intelligence can be advanced.

But improvements in much understanding may also follow from looking at the behavior of other decentralized intelligence systems such as those found in social insects. A hive is able to convey to its workers that they should collect pollen instead of nectar; when plants are short of water they increase root growth, when short of light they increase shoot growth (Bloom et al. 1985). In the case of the hive fairly simple alterations in communication are sufficient and certainly changes in abscisic acid perception help to increase root growth. But up until now this has only rarely been interpreted in plants as increased exploratory requirements.

It is obvious that at present we should regard primate intelligence as much more advanced than that exhibited by plants. But once we can identify how well an individual plant performs “in its own particular environment” and enables “one species to dominate and exert power over other species” that Warwick (2001) considers to be aspects of intelligence, this conclusion may well need reassessment.

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